LATE CAINOZOIC BRACHIOPODS FROM THE COAST OF NAMAQUALAND, SOUTH AFRICA

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ABSTRACT. An unusual late Tertiary – early Quaternary brachiopod assemblage from shallow water shoreline deposits on the Namaqualand coastal plain of South Africa is described. New species described are *Kraussina rotundata*, *K. laevicostata*, *K. cuneata* and *Cancellothyris platys*, with subspecies *C. platys platys* and *C. platys petalos*. *In situ* specimens, shell growth, abrasion and epizoans all indicate crowded living conditions, commonly on bedrock. Diversity, shell size and shell thickness are consistent with waters having been warmer than in the region today; Atlantic cooling took place from the late Tertiary.

TERTIARY and Quaternary brachiopod faunas are poorly known throughout the world, with a few notable exceptions, such as those from New Zealand or the Mediterranean. Their presence, commonly in shallow marine sediments, can provide important evidence about the marine conditions of their locations during this period of major temperature and sea-level fluctuations. We were delighted, therefore, to be presented with a well-preserved late Cainozoic brachiopod fauna from Namaqualand, South Africa, particularly as it contains representatives of genera much larger than any seen hitherto, and the *in situ* relationship with the bedrock of some species allows the formulation of well-founded palaeoecological conclusions. Faunas such as this help our understanding of the origins of Recent brachiopods and we are able to suggest possible connections between this fauna and the Recent brachiopods of southern Africa.

Since the discovery of diamonds on the west coast of southern Africa (Wagner and Merensky 1928), considerable attention has been given to the nearshore marine sediments of late Tertiary to early Quaternary age, including papers on their contained fossils. Haughton (1932) presented an overview of the west-coast deposits, and described a number of mollusc species and the brachiopod *Kraussina lata*. Since then, papers by Carrington and Kensley (1969), Kilburn and Tankard (1975), Kensley (1972, 1977) and Kensley and Pether (1986) have added to the knowledge of the molluscan fauna.

This project started in the mid 1970s when Dr A. J. Carrington presented one of us (C.H.C.B.) with a small collection of brachiopods, thought to be of Pliocene to Pleistocene age, collected during diamond exploration on the Namaqualand coast. Because data on their provenance were not available, work on the specimens ceased until Dr B. Kensley and Mr J. Pether presented us with well-documented comparable material from the same region.

This paper describes seven brachiopod species belonging to three genera which were recovered during diamond-mining activities on the three properties Koingnaas, Hondeklip and Avontuur A in the Hondeklip Bay area of Namaqualand coast (text-fig. 1).

Geological Setting. Over the years a number of authors have described and interpreted the Cainozoic coastal stratigraphy of the South African west coast. In particular, papers by Carrington and Kensley (1969), Tankard (1975) and Hendey (1981*a*, *b*) have helped to elucidate the succession and determine the depositional environments. In this paper we follow the scheme of Pether (1986*a*), who has summarized and revised the previous work. Pether's brachiopods were recovered from two regressive sedimentary units that are at present included in the Alexander Bay Formation (South African Committee for Stratigraphy 1980; Pether 1986*a*). Within each unit, named after the immediately preceding transgressive altimetric maximum, Pether (1986*a*) has recognized lower

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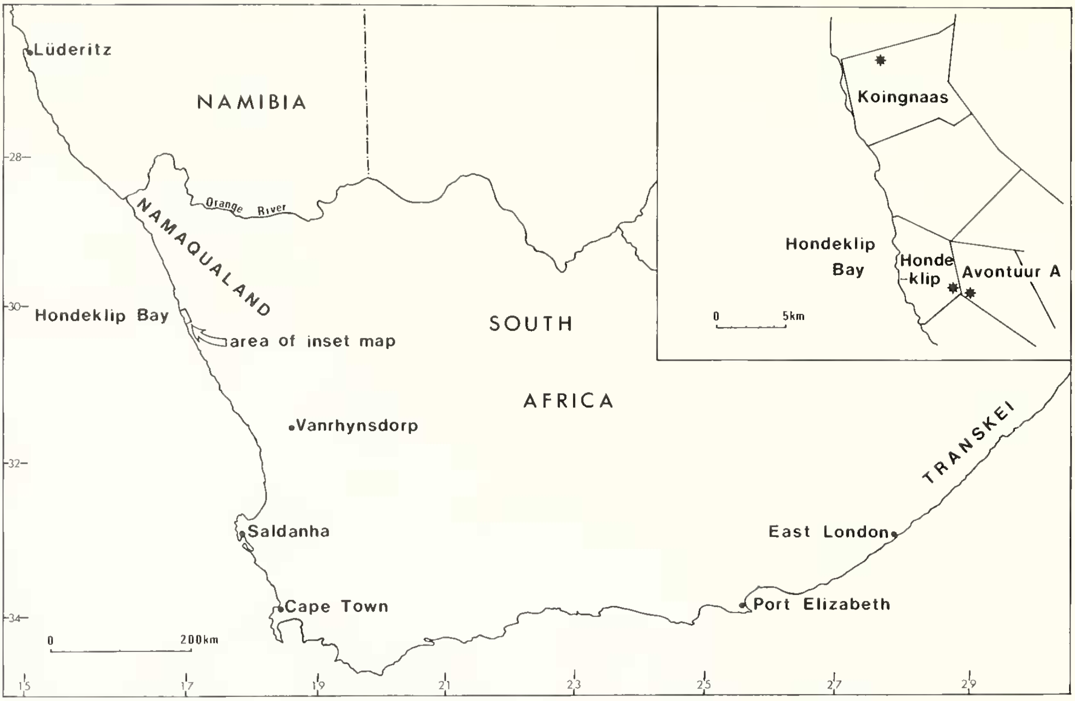
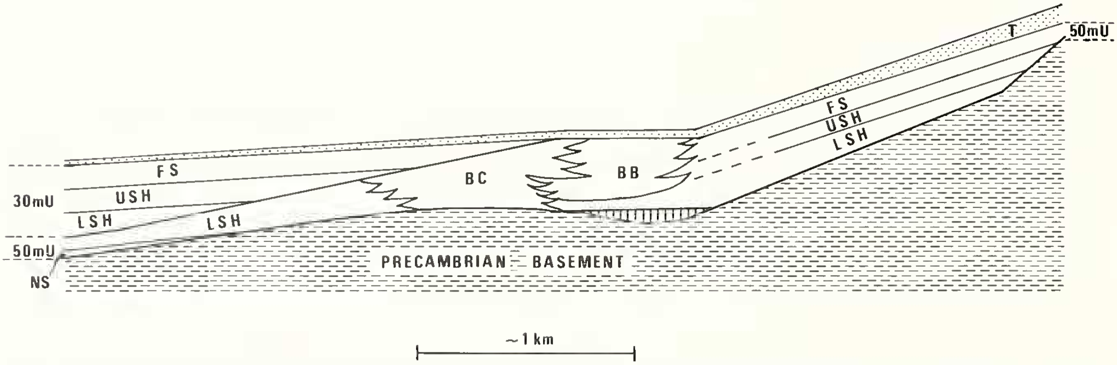


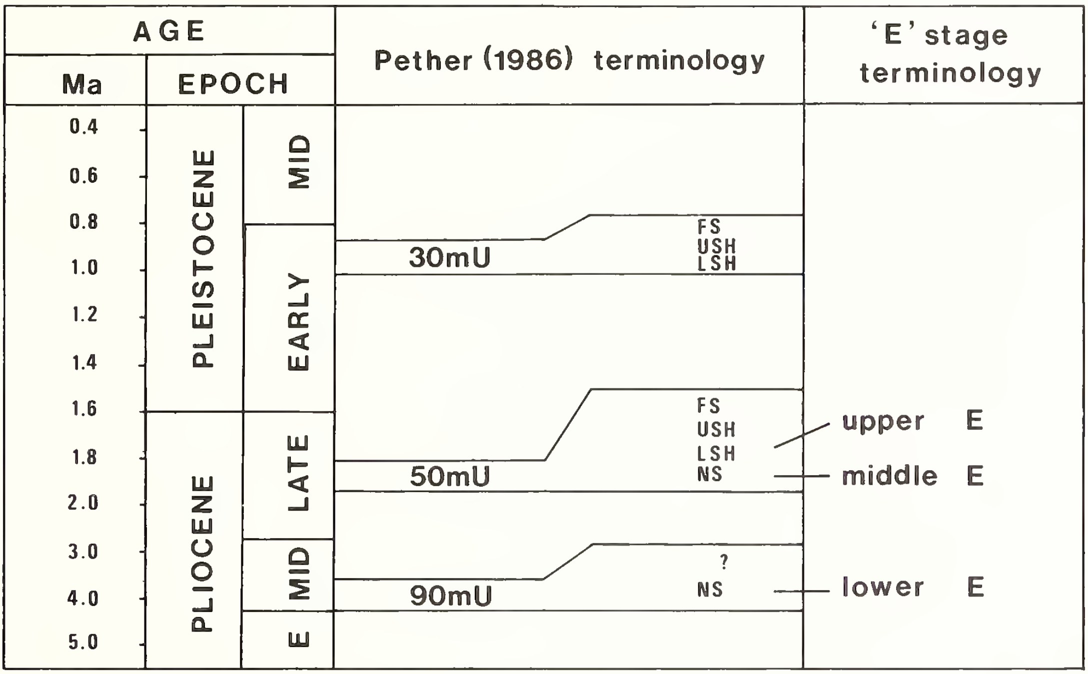
TEXT-FIG. 1. Locality map with inset showing the positions of the main collecting localities (stars).



TEXT-FIG. 2. Schematic cross-section showing the stratigraphic relationships of the two regressive sedimentary units (after Pether 1986*a*). T = younger terrestrial deposits; FS = foreshore facies; USH = upper shoreface; LSH = lower shoreface; NS = nearshore shelf; BB = back-barrier; BC = barrier complex. Vertical lines indicate an erosional remnant of a nearshore shelf deposit belonging to an earlier (mid-Pliocene) 90 m Unit.

shoreface, upper shoreface and foreshore facies (text-fig. 2). The older 50 m Unit, which rests on an eroded Precambrian gneissic basement, also contains sediments interpreted as belonging to a barrier complex, including tidal inlet deposits, and back-barrier environments. Pether (pers. comm. 1986) has reported that brachiopods are found scattered throughout the sands belonging to both units, but those in the 50 m Unit are better preserved than those in the 30 m Unit, having suffered less breakage and abrasion before burial. This may reflect the higher energy open coast conditions prevailing during deposition of the younger unit compared to the more sheltered, quieter conditions of the partially barred coast during deposition of the 50 m Unit (see Pether 1986*a* and text-fig. 2).

The only information with the Carrington specimens are markings indicating the mid or upper E stage and the Koingnaas locality, where mining exploration was proceeding at that time. The E Stage terminology was introduced by mining geologists and has been variously correlated during subsequent years, but here we follow Pether (1986*a*; see our text-fig. 3). The Carrington collection is less well preserved than the more recently collected material from Pether, and some was probably reworked in the Upper E Stage. Unless specifically mentioned, the descriptions of species are based upon the Pether collections.



TEXT-FIG. 3. Correlations of terminology and ages of the sedimentary units recognised in Namaqualand, based on Pether 1986*a*.

Age of the fauna. The precise age of the Cainozoic deposits of Namaqualand has been the subject of debate for some time. In the earlier literature a broad late Tertiary – Recent age was considered good enough, but Carrington and Kensley (1969) concluded, on the basis of their mollusc studies, that both of the regressive units described above were of Pleistocene age. Later work by Tankard (1975) and Hendey (1981*a*, *b*) suggested that these deposits were of Pliocene age. Kensley and Pether (1986) and Pether (1986*a*) have re-examined the evidence and on the basis of the percentage of extant species in the molluscan fauna, along with comparisons with the Neogene and Quaternary sea-level curves of Vail and Hardenbol (1979) and Beard *et al.* (1982), they concluded that the 50 m Unit is of late Pliocene age and the 30 m Unit can be dated as early Pleistocene (text-fig. 3). More recently, the recovery of a vertebrate fossil renders this interpretation problematic and Pliocene ages for both units must be considered (Pether 1986*b*).

THE BRACHIOPODS

The late Pliocene – early Pleistocene brachiopod fauna of the Namaqualand coastal plain is a very conservative one, but even so the diversity appears to be a little greater than that of the brachiopod fauna occupying a similar position offshore at the present time. The late Tertiary – early

Quaternary fauna comprises seven species compared to only four found in water less than 20 m deep around the southern African coast today, namely *Terebratulina abyssicola* (Adams and Reeve, 1850), *Megerlina pisum* (Lamarck, 1819), *Discinisca tenuis* (Sowerby, 1847) and *Kraussina rubra* (Pallas, 1766). Of these four, the first two are apparently confined to the warmer waters of the east coast, *D. tenuis* is found only in the cold waters along the Namibian Coast, and *K. rubra* ranges from west to east coasts (Penrith and Kensley 1970). This last-named species seems to be the only element of the fossil fauna to have survived to the present, perhaps as a result of its greater range of temperature tolerance.

Phyletic relationships of the various members of the fauna are difficult to establish. The Kraussinidae are regarded as rapidly evolved neotonous forms that appeared with apparent suddenness in the Upper Tertiary (Asgaard 1986). Recently Collins *et al.* (1988) have used immunological techniques on skeletal macromolecules from Recent brachiopods to suggest affinities within the terebratulids. Their study indicated a close relationship between *Kraussina* and *Megerlia*, followed by a relationship with *Argyrotheca*, as might be expected from current classification, all three being terebratellaceans. The earliest *Megerlia* specimens are Miocene with *Kraussina*, here described, already established by late Pliocene. Elliott (1949) for Recent *Megerlia*, and Ruggiero (1985) for Pleistocene *Megerlia* from southern Italy, have shown that the earliest brachidium in brachial valves up to about 5 mm wide is a simple V-shaped structure similar to that of adult *Kraussina*, hence the suggestion of neotenous development.

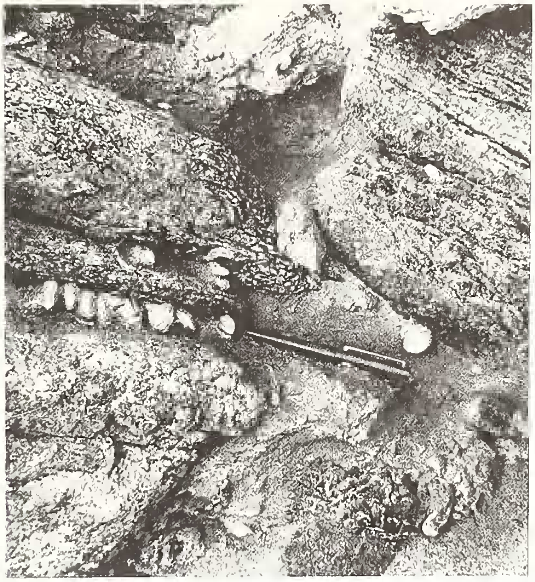
Collins *et al.* (1988) further suggested that the next level of relationship for these terebratellaceans is with terebratulaceans, such as the living *Gryphus* and *Liothyrella*. This break from the usual classification is challenging. However, the immunological work is in its infancy and this result may prove false; certainly their study, if accepting the above derivation of *Kraussina* from a *Megerlia*-like species, has to explain the derivation of a terebratellacean loop in *Megerlia* from the short-looped terebratulaceans, within which are few known wide hinged, strongly costate Mesozoic shells looking at all as if they could have given rise to the kraussinids. Possibilities would seem to be limited to *Meonia* and similar cancellothyrids. The alternative opinion of derivation from the long-looped terebratellaceans might lead to investigation of species like the late Cretaceous (?dallinid) *Gemmarcula*. The South African Cretaceous and Palaeogene brachiopod faunas, best known from the eastern coastal regions, are not known to contain any terebratellaceans.

K. lata Haughton, 1932 and *K. laevicostata* sp. nov. are recorded from only the 50 m Unit, so they do not seem to extend into the Pleistocene. *K. rotundata* sp. nov. is tentatively recorded from the 30 m Unit, as well as the 50 m Unit and thus ranges from the Pliocene into the Pleistocene. *K. rubra* can be taken as extending from the Pliocene to the Recent; it occurs in Cape waters along with *K. crassicostata* Jackson, 1952 and the poorly known *K. cognata* (Sowerby, 1847), a species almost devoid of ribs. Thus there is, at present, a gap in the geological record of *Kraussina* in South Africa equivalent to the middle and late Pleistocene, and it is during this period that any possible connections between the fossil and extant forms must exist. On the basis of its fairly coast ribbing and quite convex shape, one might suggest that *K. crassicostata* is derived from *K. lata*, but evidence for this connection is lacking.

Palaeoecology

Most of the specimens were recovered from sands deposited in an upper-lower shoreface setting which Pether (1986*a*) interprets as representing water depths of 1·5 m to 10 m. The associated biota includes crustaceans (crabs and barnacles), gastropods, bivalves, scaphopods, polyplacophorans, an occulinid coral, bryozoans, foraminifera, and possible sedentary polychaetes.

Rare occurrences of specimens in life position are known (text-fig. 4). *Kraussina rotundata* sp. nov. and *Cancellothyris platys platys* subsp. nov. have been found *in situ* in crevices in the Precambrian bedrock where they tend to form species clusters, although the two occur in close association. Evidence from the collected and studied specimens indicates that *K. rotundata* lived more commonly within these crevices than *C. platys*, especially at the Koingnaas locality. In this area almost all specimens of *K. rotundata* have abraded posterior regions; in some it is so severe as



TEXT-FIG. 4. Photograph showing specimens of *Kraussina rotundata* sp. nov. in life position in crevices in Precambrian bedrock exhumed as a result of diamond mining activity. The locality, on Avontuur A, represents a palaeodepth of 4–5 m near the upper shoreface/lower shoreface boundary. The pen is approximately 150 mm long.

to have removed part of the cardinal process and part of the sockets and teeth. This has led to the enlargement of the pedicle aperture, but in life much of this opening would have been closed by a tough 'skin' surrounding the actual pad-like pedicle. This 'skin' incorporated muscles which attached to the pedicle collar and these, along with the extensive adjustor muscles (see *K. rotundata* description) moved the shell around the pedicle and, by contraction, held the shell tightly to the substrate in a closed condition. Many of the shells display abraded areas on their flanks where the valves moved against rock, while opening and closing. Others display growth distortion as a result of growth around either neighbouring shells or protruding rocks (text-fig. 6A–C; Pl. 3, figs. 12–16). The intense nature and local distributions of these abrasions and distortions shows that they occurred during the life of the brachiopod, rather than after death, and this is further supported by the good preservation of other areas of valve surface. Similar, closely clumped associations of living *K. rubra* are to be found (text-fig. 5G, H) in which younger shells are attached to older individuals which attached to rocks or pebbles. In these situations the individual shells display a little distortion and abrasion of the ventral umbo, but in comparison to the crevice dwelling *K. rotundata*, they are free to move in open water.

Cancellothyris specimens display less abrasion and distortion. This may be because of their different pedicles. Unlike *Kraussina*, the pedicle of living *Cancellothyris* is long and narrow, furnished with contractile muscles and the ability of adjusting the growing shell to constraints in its immediate environment. The shell of *Kraussina* could not lift much above its original attachment point, whereas *Cancellothyris* could, thus enabling its valves greater freedom of growth and movement. Presumably the slight abrasion of the pedicle aperture seen on some *Cancellothyris* occurred while the shells were held down onto the substrate when closed and 'avoiding danger'. On other specimens there are patches of abrasion on the flanks posteriorly, commonly affecting both valves, indicating that the umbos were probably attached within a rock crevice. More rarely, in some specimens short lengths of their lateral commissures have growth distortions which have produced cavities (Pl. 4, fig. 11). Within these the growth lines developed normally, although somewhat accentuated, but the normal geometry of shell secretion was interrupted by some hard object impinging on the edges of the shell. The internal surfaces of the valves in these areas, apart from being internally convex, appear normal. From the dispositions of the growth lines in these cavities it would seem that biological interference with the valve margins did not take place, but that as the shell grew, a short length of its margins was increasingly prevented from normal growth. A protrusion from the edge of the rock crevice in which the specimen grew seems the most likely cause.

Another feature, seemingly related to the close hold-fast nature of the *Kraussina* pedicle and the abrasion of shell affecting the articulation, is the anterior zig-zag commissure. A commissure of this sort provides great stability to the positioning of the valves when closed and resists torsion between the valves. Normally, terebratulid articulation is sufficiently strong to resist any torsion between the valves, but in those specimens that have weakened articulation, through shell abrasion, the zig-zag commissure must have been helpful in aiding stability. In two examples, severe posterior abrasion has led to a slight dislocation of one valve relative to the other so that the anterior commissure apparently no longer fitted exactly, although the ribs of one valve still partially interlock with the interrib spaces of the other valve.

Some species range down into the distal lower shoreface and nearshore shelf environment, and *Kraussina laevicostata* sp. nov. and *Cancellothyris platys petalos* sp. et subsp. nov. appear to be confined to this deeper water niche. Table 1 shows the distribution of the fossil brachiopods between the two sedimentary units. This indicates that all seven species are found in the older 50 m Unit, whereas only three are known from the 30 m Unit. Commenting on the diversity contrast between the two units, Kensley and Pether (1986) state that the higher diversity of the 50 m Unit, also

TABLE 1. Species of brachiopods from three localities in the Hondeklip Bay area of the Namaqualand coast, showing the regressive unit and depositional facies from which they were obtained. USH = upper shoreface; LSH = lower shoreface; NS = nearshore shelf.

	50 m Unit			30 m Unit	
Species	USH	LSH	NS	USH	LSH
Cancellothyris platys platys sp. et subsp. nov.	X	X	X	X	X
Cancellothyris platys petalos sp. et subsp. nov.	.	.	X	.	.
Kraussina rubra	X	X	X	X	X
Kraussina laevicostata sp. nov.	.	.	X	.	.
Kraussina lata	.	X	X	.	.
Kraussina rotundata sp. nov.	X	X	.	.	X(?)
Kraussina cuneata sp. nov.	.	X(?)	.	.	.
Pelagodiscus (?) sp.	X	X	.	.	.

EXPLANATION OF PLATE 1

Scanning electron micrographs of borings and encrusters.

Figs. 1 and 2. *Cancellothyris platys platys* sp. nov. brachial valve interior. BD6757. 1, part of the posteromedian region, with part of the cardinal process on the right and one crus extending to the bottom edge, showing the blistered appearance of the valve floor resulting from intense boring from the outer surface. × 12. 2, an enlargement of the valve floor showing shell mosaic, endopuncta and the irregular, blistered shell growth. × 80.

Figs. 3–8 are all examples of *Kraussina rotundata* sp. nov. with various encrusters and borers. 3, an example of the foraminifera *Cibicides lobatulus* (Walker and Jacob) adhering immediately anterior to a growth line. BD6719. × 64. 4, a cluster of the bryozoan *Hippothoa* in an interrib space. BD6720. × 55. 5, part of a colony of the sheet-like bryozoan *Celleporella* growing away from the valve margin (bottom left). BD6716. × 24. 6, part of the bryozoan *Tubulipora*, associated with *Hippothoa*, on the mid region of a brachial valve. BD6715. × 24. 7, the mid-lateral region of a brachial valve from which much of the primary shell layer has been removed by 'grazing', perhaps with the destruction of the edge of the *Celleporella* colony. *Hippothoa* has grown onto the 'grazed' area. BD6716. × 23. 8, the thick-shelled umbonal area of the brachial valve with excavated pits showing some signs of marginal chipping or scratching. The abraded umbo is to the top right. BD6716. × 22.

PLATE 1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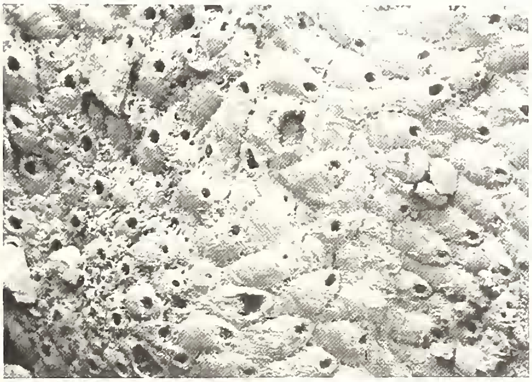
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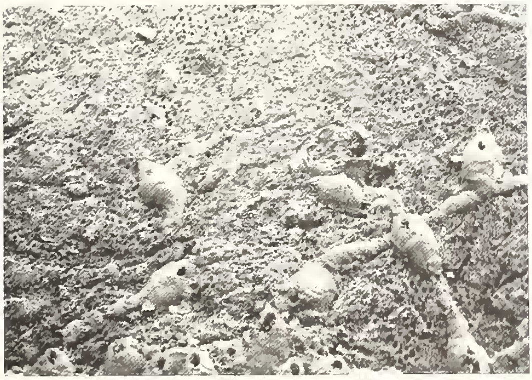
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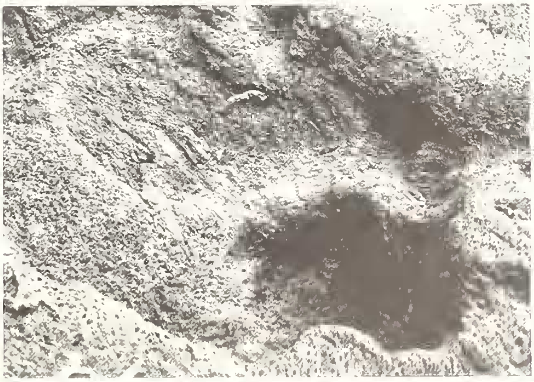
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BRUNTON and HILLER, Namaqualand brachiopods

reflected in the molluscan fauna, is either real or is possibly an unavoidable bias due to the nature of the available exposures.

The reduction in diversity from the 50 m Unit to the 30 m Unit through to the present time possibly reflects a gradual reduction in water temperatures. Kensley and Pether (1986) document the presence of warmer water West African and east coast forms among the fossil molluscs from Hondeklip Bay. On this basis they concluded that the two sedimentary units were deposited in waters significantly warmer than at present and, although the evidence is not clear-cut, they inferred a cooling trend over the period of deposition of the two units. Dingle *et al.* (1983) have summarized the available data on South African Neogene and Pleistocene palaeoclimates. These point to a general cooling from the time the upwelling of cold central Atlantic water in the Benguela Current system was established in Upper Miocene times (Siesser 1978). The most intense upwelling occurred during the Pleistocene and surface water temperatures reached a minimum during the last glacial maximum (Embley and Morley 1980). Detailed localized palaeotemperature data from oxygen isotope analysis of fossil oyster shells from the Hondeklip Bay area are still awaited.

All the species in this fauna attached themselves to the substrate by means of a strong functional pedicle and were thus well adapted for living in high energy shallow water conditions. All the species other than *K. cuneata* are larger than other known representatives of these genera, and the shell material in *K. lata*, *K. laevicostata* and to a lesser extent in *K. rotundata* is much thicker than met with elsewhere. The secretion of abundant calcium carbonate in shell material is associated with waters warmer than now found off Namaqualand.

External encrusters, grazers and borers

Many of the well preserved specimens, especially *K. rotundata* from Avontuur, have bryozoans, foraminifera and rare arenaceous tubiculous polychaetes encrusting their surfaces. Less commonly, specimens have been abraded or bored by organisms.

The commonest encrusting bryozoan is the ascophoran cheilostome, *Hippothoa*, a chain-like and branching form having a distal orifice with a sinus (Pl. 1, figs. 4, 7). Less commonly the ascophoran sheet-like genus *Celleporella* (Pl. 1, fig. 5) and stem-like hexagonally patterned *Tubulipora* (Pl. 1, fig. 6) are preserved, but abraded. Living species of these genera are characteristically epiphytes, living on algae, but they also encrust stones and shells.

Hippothoa commonly can be seen to have originated posteriorly, on either valve, and grew essentially anteriorly, as the brachiopod grew. In strongly ribbed areas the bryozoan grew mostly in the interrib spaces (Pl. 1, fig. 4) and, less commonly, transversely within the 'step' of major growth lines. Overgrowth is quite common and where a valve is shared also by *Tubulipora* they overgrew each other, although anteriorly the latter overgrew *Hippothoa* more frequently, as well as individual *Cibicides* foraminifera. Only one shell has an extensive colony of *Celleporella* (Pl. 1, fig. 5).

There is no bryozoan encrustation on any of the areas of physical abrasion on *K. rotundata*, indicating that the bryozoans grew on the brachiopods while living in their rock crevices. There is, however, some sign (Pl. 1, fig. 7) of *Hippothoa* growing on areas which appear to have been abraded by grazing benthos (see below). The flattened, normally attached foraminifera *Cibicides lobatulus* (Walker and Jacob 1789) is found both adherent to outer surfaces of these brachiopods (Pl. 1, fig. 3) as well as loose within the sands filling some shells. This species is known on Recent algae, but on *Kraussina* lived between ribs or below the 'steps' of major growth lines near the margins of shells.

Kraussina and *Cancellothyris* specimens display scratch marks resembling those made by the radula of chitons or by echinoids while grazing. The normal valve exterior probably was not attractive to grazers, but if acting as the substrate for algae, sponges, or bryozoa, these surfaces may have provided valuable nutrient (Pl. 1, fig. 7). None of the above encrusters, nor signs of grazing abrasion, have been found on inner valve surfaces, so most, if not all, the associations occurred during the life of the brachiopods.

Most species, but especially *Cancellothyris*, display borings from the valve exteriors which, in some specimens (text-fig. 10E), has resulted in the removal of the complete external surface over considerable areas. These areas start as a series of minute holes dispersed over a circular area (text-fig. 10D, E) about 1·5–2 mm in diameter. Progressive removal of shell led to the pitted, corroded surface of extreme examples. Many of these borings appear to have gone sufficiently deeply into the shell material to have affected the mantle epithelia, which reacted by secreting extra shell material over the areas involved. The resultant inner surface is clearly thickened, somewhat irregular and tending towards a blistered appearance (Pl. 1, figs. 1 and 2). Such a sequence of events shows that the borings occurred during the life of the brachiopod.

Other elongate trough-like borings, at the ends of which are small (*c.* 0·5 mm) circular holes penetrating the valve thickness, occur rarely (Pl. 2, figs. 9 and 10). Several *K. rotundata* specimens are excavated posteriorly, where the shell is thick, leaving pits up to 5 mm in diameter penetrating up to 2 mm into the shell substance. The edges and bottoms of these may display marks which appear to be scratches left by a predator (Pl. 1, fig. 8). Their disposition makes it unlikely that they were produced by echinoids.

Apparently confined to *Cancellothyris* specimens are microscopic boring ramifications attributed to microscopic marine algae or fungi. The extent of infestation varies from a few patches posteriorly to most of the shell substance. These borings would seem to have invaded the thick shell at the umbos and sockets and to have spread anteriorly from there. Although they extend through the shell thickness they are best seen just below the relatively smooth internal surfaces, and we feel that the endolithic microorganism is more likely to have invaded after the brachiopod's death.

The grazings and some borings removed shell material during the brachiopod's life. The endolithic ramifications, where intense, weakened the general shell fabric, so that in concert with the loss of organic material (fibre sheaths etc.) from the secondary layer, the shell material was weakened and made vulnerable to physical degradation. Collins's (1986) study of taphonomy in a moderately-deep brachiopod community showed how the shell of Recent *Terebratulina* weakened over a period of about 200 days, becoming increasingly liable to physical breakage. This was attributed to the loss of organic material, perhaps resulting from the action of moulds or bacteria. Thus the occurrence of many of these brachiopods, from a shallow-water environment yet in a good state of preservation, is surprising, and we suggest results only from rapid burial by the regressive sands in which they occur.

Biogeography

The dominant genus is *Kraussina*, endemic to African, especially southern African, waters at the present time. The only previous fossil records of the genus are also from South Africa. A rather unexpected connection with the Australian region comes in the form of *Cancellothyris* which is not known from off South Africa at the present, but occurs in Australian waters. A Miocene species is recorded from New Zealand. *Pelagodiscus* is a very widespread genus in the modern oceans, although it usually occurs in deep waters. However, possible shallow water fossil species are described from Belgium and England.

At the species level, four members of the fauna described herein are named as new species, one cannot be named because of insufficient material, and two previously described species, *K. lata* and *K. rubra*, are known only from South Africa. Thus it may be concluded that the Namaqualand brachiopod fauna is endemic, although there is a possible connection with the Australasian region. One of the extinct gastropods from the 50 m Unit, *Argobuccinum casus*, is also linked to that region (Pether pers. comm. 1986).

SYSTEMATIC PALAEONTOLOGY

Specimens are housed in the British Museum of Natural History, London (BD and ZB registration numbers), or the South African Museum, Cape Town (SAM numbers).

Class INARTICULATA Huxley, 1869
Superfamily DISCINACEA Gray, 1840
Family DISCINIDAE Gray, 1840
Subfamily DISCINISCINAE Schuchert and LeVene, 1929
Genus PELAGODISCUS Dall, 1908

Pelagodiscus(?) *sp.*

Text-fig. 5A–F

Material and horizon. A total of thirty-one brachial valves plus some fragmentary material that may include parts of pedical valves, from the 50 m Unit on the farm Hondeklip.

Description. Small subcircular brown phosphatic shells; brachial valves are conical with the apex more or less centrally situated, or slightly posterior of centre. The outline is almost circular, although many specimens display an almost straight posterior margin. Height of the cone is equal to about one-half of the shell diameter. In profile, the posterior slope is slightly shorter and steeper than the anterior slope. Ornament of irregular concentric growth lines, but one specimen displays faint radial ornament developed after the shell attained a diameter of 4·3 mm. The pedicle valve is unknown.

Dimensions. Typical dimensions (in mm) of specimens are as follows, where a = anterior to posterior diameter, b = left to right diameter, c = height of cone.

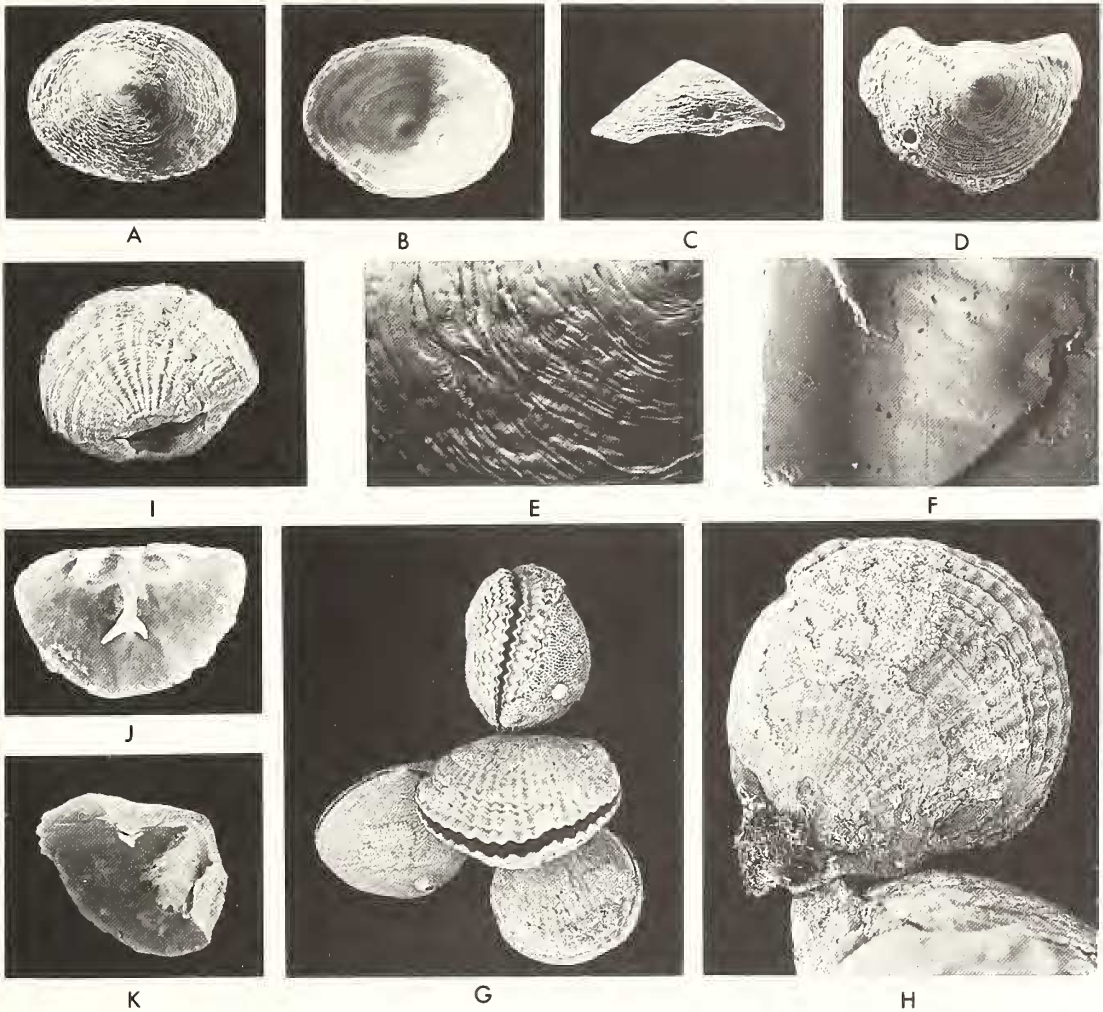
	a	b	c
SAM PQ HB 913	10·6	10·4	5·8
	12·3	11·9	6·0
	14·8	12·4	6·8
	11·3	10·9	5·3
SAM PQ HB 662	8·5	8·6	4·5
	6·0	6·9	3·2

Discussion. The specimens described here are tentatively assigned to *Pelagodiscus* on the grounds that the overall morphology of the brachial valve is virtually identical to that of the type species, the living *P. atlanticus* (King 1868). The various extant species of the closely related genus *Discinisca*, all tend to have the apex of the cone more posteriorly situated or they have a marked radial ornament. However, the main difference between these genera is in the form of the lophophore, with *Pelagodiscus* possessing a schizolophe while that of *Discinisca* is spirolophous. Thus, without the soft parts it is impossible to be unequivocal about the current assignment.

The earliest-formed shell of some limpets living off South Africa resemble these shells, but we reject them for two reasons. There is no sign of twist to their umbos, as seen in the molluscs, and secondly, the shell material is a mineral virtually unknown amongst molluscs. Infra-red spectrum and X-ray analysis indicates that the shell material is a carbonate-fluorine-hydroxy substitute apatite, similar to Dahllite. The presence of chitin was not clearly demonstrated by the analysis, but may have been screened.

Fossil *Pelagodiscus* are poorly known. Thomson (1927) included in the genus two Tertiary species; *Discina suessi* Bosquet 1858 from the Lower Miocene of Belgium, which he included tentatively, and *Discina fallens* Wood 1874 from the Crag deposits of East Anglia, England which are of late Pliocene–early Pleistocene age. If the latter is indeed a *Pelagodiscus* then it represents another shallow water species.

P. atlanticus is perhaps the most widespread of all living brachiopod species, living mostly in the depths of the abyssal and lower bathyal regions. Its overall depth range is given as 366–5530 m, although empty shells have been found as deep as 7600 m in the Romanche Trough in the Central Atlantic (Zezina 1980). The recovery of the specimens described here from shallow water sediments would indicate that they occupied quite a different habitat one to two million years ago than the living species. Another difference between the two is in their size; most known specimens of *P.*



TEXT-FIG. 5. A–F, *Pelagodiscus* sp. from Hondeklip. A–B, a brachial valve exterior and interior, BD6670. ×3. C–D, a brachial valve viewed laterally and dorsally, BD6671. ×3. E, detail of the external ornamentation, near the brachial valve apex, scanning electron micrograph (uncoated), ×23. F, detail of the brachial valve interior, close to the margin, showing the smooth but slightly grooved surface. SEM (uncoated), ×37. G and H, *Kraussina rubra* (Pallas), from the Agulhas Bank, South Africa, at 22 fathoms. J. W. Jackson collection, ZB2240–43. G, clump of four specimens. The specimen at the top appears to have been attached to sponge, the central specimen is attached to the first and the remaining two are attached to the central one. ×1. H, detail of the central specimen's attachment to the first specimen; note the tight fit of the pedicle aperture onto the substrate, here the umbo of another specimen. ×2. I–K, *Kraussina rubra* (Pallas), from Koingnaas, BD6677, ×2; posterodorsal view of the complete shell, the brachial valve interior, and the pedicle valve viewed posterodorsally.

atlanticus have a diameter in the range 3–5 mm, whereas these fossil specimens are larger with some exceeding 13 mm in diameter. Thus it seems that relatively large Cainozoic shallow-water species migrated to deeper water, and became smaller, during the last two million years.

Class ARTICULATA Huxley, 1869
Superfamily TEREBRATELLACEA King, 1850
Family KRAUSSINIDAE Dall, 1870
Genus KRAUSSINA Davidson, 1859

Type species. Anomia rubra Pallas 1776, designated by Davidson 1853, for *Kraussia* Davidson 1852, but renamed in 1859 (see text-fig. 5G, H).

Diagnosis. Ventribiconvex, rounded to transverse, broad hinged, multicostate to (rarely) smooth shells. Cardinal process low, broad. Dorsal median septum supporting pair of stout ventrolaterally projecting arms of brachidium.

Discussion. Until now, with few exceptions, *Kraussina* species have only been found from present seas around southern Africa. In that region there are four named species in addition to the type: *K. cognata* (Sowerby 1847), *K. gardineri* Dall 1910, *K. mercatori* Helmcke 1939, and *K. crassicostata* Jackson 1952. The only named fossil species, *K. lata* Haughton 1932, also came from South Africa, somewhat south of, but of about the same age as, the present fauna. Thus *Kraussina*, as presently known, is strongly endemic to seas around southern Africa.

It is noteworthy that we propose five species of *Kraussina* for the Pliocene/Pleistocene seas off south-west Africa (*K. rubra*, *K. lata*, *K. rotundata sp. nov.*, *K. laevicostata sp. nov.*, and *K. cuneata sp. nov.*), the same number as named in today's waters. Although the time span of the older 50 m Unit, from which all five species were collected, may be about half a million years, the number of species apparently living in the same region is surprising. We suggest, however, that the late Tertiary was a period of evolutionary radiation for *Kraussina*, with only *K. rubra* continuing to the present. *K. lata* could well have evolved into *K. crassicostata*, while *K. rotundata*, with further loss of ribbing, may have become *K. cognata*.

Kraussina rubra (Pallas, 1766)

Text-fig. 5I–K

1766 *Anomia rubra* Pallas, p. 182, pl. 14, figs. 2–11.
1952 *Kraussina rubra* (Pallas); Jackson, p. 22, pl. 3, figs 1 and 2.
1986 *Kraussina rubra* (Pallas); Hiller, p. 129, fig. 16.

Material and horizon. Five conjoined valves, two pedicle valves and three brachical valves from the 50 m Unit on Hondeklip, Avontuur A and Koingnaas plus six pedicle valves and one brachial valve, as well as fragmentary material, from the 30 m Unit on Hondeklip.

Description. Biconvex shells with variable transversely oval outlines. The hinge line is nearly straight, almost nine-tenths as wide as the valve. The anterior commissure is rectimarginate to broadly and very gently sulcate. The beak is suberect and irregularly truncated by a large incomplete submesothyridid foramen. The palintropes are triangular, bounded by the foramen and beak ridges. Ornament consists of concentric growth lines and strong rounded ribs which may increase by branching or intercalation; ribbing density is of 2–6 ribs, most commonly 3, in a 5 mm sector at the 10 mm growth stage.

The pedicle valve is gently convex in lateral profile but strongly convex, especially medianly, in anterior profile. Brachial valves are gently convex in lateral profile; in anterior profile they are flat or gently sulcate medianly, with gently convex flanks.

Pedicle valve interiors have small teeth, without dental plates; a pedicle collar, where preserved, is very short and sessile. Other details are obscure. Brachial valve interiors have widely divergent socket ridges bounding narrow sockets. A small cardinal process is situated between the poterior ends of socket ridges in small specimens but is reduced by abrasion in large specimens. The notothyrial platform consists of a pair of suboval thickenings between the socket ridges and the posterior end of the median septum; rounded depressions on the platform mark the sites of attachment of pedicle muscles. A low median septum extends anteriorly from the notothyrial platform and supports, at its distal end, a pair of ventrally divergent lamellae. The rest of the brachidium is unknown. Small submarginal tubercules are present in some specimens.

Dimensions. Dimensions of conjoined valves are (in mm):

	Length	*Width*	*Thickness*
SAM PQ AV 610	14·9	16·9	9·1
	19·6	19·8	10·5
SAM PQ HB 217	14·9	17·8	9·6
	17·0	17·3	10·8
	18·1	20·4	12·6

Discussion. A small proportion of the kraussinids recovered from the 50 m Unit can probably be assigned to *Kraussina rubra* (Pallas 1766), and it seems that most of those from the 30 m Unit can be similarly assigned. We describe our material since it differs slightly from the living specimens upon which all previous descriptions have been based. The most tangible difference is that the fossil shells tend to be slightly more coarsely ribbed. A small sample of *K. rubra* recovered live from off the southern Cape coast gave figures of 3–6 ribs per 5 mm sector at the 10 mm growth stage on one, thirteen, twenty-two and four shells. Comparable figures for the fossil material described here are 2–6 ribs on two, eight, seven, six and one shells. This difference is thought not to be significant.

Fossil *K. rubra* has been found in shallow marine deposits of late Tertiary to early Quaternary age in other places around the South African coast. Haughton (1932) listed the species from limestone quarries at Hoedjies Bay, near Saldanha, about 300 km south of Hondeklip Bay. In the same area Kensley (1972) recorded it from the 'E' quarry at Langebaanweg and it is known from the Alexandria Formation, a late Pliocene – Pleistocene shoreline deposit cropping out in the coastal areas in the vicinity of Port Elizabeth. These occurrences suggest that the distribution of *K. rubra* in late Pliocene – early Pleistocene times is very similar to its present distribution, i.e. in intertidal and shallow subtidal settings from Transkei, in the east, to Lüderitz on the Namibian coast, in the west. Fossil shells from these other areas show a similar ribbing density to the specimens described here.

Kraussina lata Haughton, 1932

Plate 2, figs. 1–13

1932 *Kraussina lata* Haughton, p. 34.

Diagnosis. Somewhat transverse, ventribiconvex *Kraussina* with strong coarse ribbing.

Type. Haughton's (1932) original material from the 'basal grit' at 'The Point', on the north side of the Olifants River, cannot be traced. We select, therefore, a brachial valve from Koingnaas, which appears to conform to Haughton's brief description, as Neotype (Pl. 2, figs. 1 and 2), BD6681.

Material. In addition to the neotype, in the Carrington collection are six pedicle valves and fourteen brachial valves. From the Pether collection there are one extra pedicle valve and four brachial valves from Koingnaas.

Description. The outline is very broadly obovate and the lateral profile strongly ventribiconvex, the brachial valve convexity largely resulting from a weak median sulcation. Pedicle valves are not folded, but the anterior commissure is weakly sulcate. The hinge line is just posterior to the widest part of the shell, but may form the widest part of the brachial valve. The pedicle aperture and interareas are characteristically wide and subject to abrasion. External ornamentation is of growth lines and strong, coarse costae, costellae being added rarely by branching. The total number of ribs varies from 8 to 16 on brachial valves, with 10 or 11 being the commonest number of costae.

Pedicle valve interiors are scarce. Teeth appear to have been short and stubby. There is a sessile pedicle collar and the muscle scars are essentially as in *K. rotundata*, but the pedicle adjustor muscle scars tend to be shorter and wider, and only narrowly separated medianly. On one specimen secondary shell growth has allowed the merger of these scars (Pl. 2, fig. 6). Submarginal tubercules are preserved on some brachial and pedicle valves.

Dimensions (in mm)	*Length*	*Width*	
Neotype b.v.	24·6	30·7	BD6681
b.v.	25·8	*c*.30·0	BD6682
b.v.	27·8	35·8	BD6683
p.v.	24·8	29·8	BD6684
p.v.	32·6	33·7	BD6685
p.v.	25·7	32·6	BD6686

Discussion. The species is the commonest representative in the collections originally presented by Carrington. Unfortunately details of locality are unknown, but some specimens are noted as from the mid or upper E Stage and marked 'A 32' (Pl. 2, figs. 3–6). No complete shell is preserved and all show signs of erosion, in some specimens this is severe and has removed structures. Also in the Carrington collection are several incomplete valves of *Kraussina* we consider as a variety of *K. lata*. These are unusually wide shells with strongly thickened brachial valves (Pl. 2, figs. 14–21) in which the pedicle adjustor muscle scars extend anterolaterally well beyond the anterior ends of the sockets. Unfortunately all these valves are badly eroded so rib counts cannot be made. However, the few remaining ribs indicate that they were more frequent than on *K. lata*; we term these specimens *K.* cf. *lata*.

As Haughton's description (1932) was so brief we have provided a full description and comparison with other species. In general outline and profile *K. lata* resembles *K. laevicostata*, and both tend to be sulcate anteriorly. They differ markedly in the strong ribbing on *K. lata*, which manifests itself also on the insides of valves. This costation, with rare added costellae, covers the valves, although their prominence decreases towards the posterior margins. This is in contrast to *K. rotundata* in which the costae are non-existent on the flanks and posterolateral areas. *K. rubra* specimens are smaller than *K. lata* and have much finer ribbing (see Table 2).

EXPLANATION OF PLATE 2

Figs. 1–13. *Kraussina lata* Haughton. 1 and 2, neotype, a brachial valve viewed externally and internally. BD6681. × 1. 3 and 4, external and internal views of a brachial valve with a series of growth distortions affecting the left posterior hinge line, the valve medianly and in its mid-length right side sector; the shell is bored posteromedianly leading to extra thickening on the right side of the median septum. Carrington collection, A32, mid to upper E stage. BD6682. 5 and 6, external and internal views of a large brachial valve with borings from the external surface producing 'blistering' of the internal surface; there is a small open canal from the pedicle adjustor muscle field to the posteroventral surface of the median septum (arrowed). Carrington collection, A32. BD6683. 7 and 8, external and internal views of a well preserved pedicle valve showing external ornamentation and the pedicle collar. Koingnaas. BD6684. 9 and 10, external and internal views of a somewhat abraded adult pedicle valve with borings, some of which broke through to the inner surface. The pedicle aperture is abraded ventrally and the muscle scars can be distinguished. Carrington collection, A32. BD6685. 11–13, external, internal and posterior views of a pedicle valve with a strongly abraded umbo and consequentially reduced pedicle collar. Carrington collection, A32. BD6686. All × 1.

Figs. 14–21, *Kraussina* cf. *lata* Haughton, Carrington collection. 14 and 15, external and internal views of a large and badly eroded brachial valve displaying posterior abrasion and external pitting, the possible result of borings; the 'ME' is for mid E stage. BD6691. 16 and 17, external and internal views of a partially eroded brachial valve with the median part of its hinge line removed by abrasion; note the anterolaterally extended pedicle adjustor scars. Upper E. BD6692. 18 and 19, external and internal views of a partially eroded brachial valve. Anteromedialy the ribbing is well preserved; the pedicle adjustor scars compare with those of fig. 15, but contrast with those of figs. 17 and 21. Mid E. BD6693. 20 and 21, external and internal views of a badly worn brachial valve, having lost all its ribbing; the anterior extension of the pedicle adjustor scars seems characteristic of the Upper E specimens. BD6694. All × 1.

PLATE 2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BRUNTON and HILLER, Namaqualand brachiopods

TABLE 2. Summary of ribbing densities on species from Hondeklip Bay plus *K. rubra* and *K. crassicostata* (Recent) from off the southern Cape coast.

	Number of ribs in 5 mm sector at 10 mm growth stage			
Species	Range	Mode	Sample Size	Age
K. rubra	3–6	5	40	Recent
K. crassicostata	3–4	3	5	Recent
K. rubra	2–6	3	24	Pliocene–Pleistocene
K. lata	2–3	3	8	Pliocene
K. rotundata	1–4	2	18	Pliocene
K. cuneata	12–16	15	12	Pliocene
K. laevicostata	'Ribs' develop only after 30 mm growth			
	at 20 mm growth stage			
Cancellothyris platys	12–17	13	26	Pliocene

Growth distortion is uncommon in *K. lata*, and although their pedicle apertures are abraded to some extent, it is never as severe as in *K. rotundata*. This indicates that *K. lata* lived attached to hard substrate but not in crowded conditions or in rock crevices.

Until now *K. lata* was the only described kraussinid from the late Tertiary to early Quaternary deposits of South Africa. Amongst living *Kraussina* in South African waters *K. crassicostata* Jackson has a similar number of costae, but it does not grow to the dimensions of *K. lata* and tends to be as wide as long. It is, however, possible that a reduction in size and relative width in *K. lata* could have resulted in the living *K. crassicostata*.

EXPLANATION OF PLATE 3

Figs. 1–16. *Kraussina rotundata* sp. nov. 1–5, holotype from Avontuur A-T3. BD6705. × 1·5. 1 and 2, the complete shell viewed dorsally and ventrally showing the median ribbing. 3, the brachial valve interior with a virtually complete brachial support. 4, the shell viewed posterodorsally showing abrasion around the pedicle opening. 5, the pedicle valve showing the teeth. 6–9, a young shell from Avontuur. BD6706. × 1·5. The shell is viewed dorsally, posteriorly, anteriorly slightly agape to show the brachial supports, and laterally; the ventral umbo is virtually unabraded. 10 and 11, a mature shell viewed laterally and anteriorly showing the extent to which the valves can open, and the lophophore supports. Avontuur, BD6707. × 1·5. 12–14, a young shell displaying considerable growth distortion and abrasion (arrowed). Avontuur, BD6708. × 1·5. 12 and 13, brachial and pedicle valve exteriors. 14, brachial valve interior showing the distorted growth of the brachidium, in which the two arms grew almost in contact medianly. 15 and 16, an almost fully grown but distorted and abraded shell. Avontuur, BD6709. × 1·5. 15, the complete shell viewed dorsally; the ventral umbo had been abraded especially on the left side, as far as the tooth. 16, brachial valve interior showing the confined growth of the hinge line. 17 and 18, an adult, strongly abraded shell. Avontuur, BD6710. × 1·5. 17, oblique lateral view showing severe abrasion at both umbos and flank of the pedicle valve. 18, dorsal view showing median abrasion to the extent that the dorsal median septum shows through the remaining shell (arrowed). 19 and 20, a brachial valve viewed externally and internally from the Carrington collection, Upper E. BD6711. × 1. 21–24, an abraded (right side of the ventral umbo) and posteriorly bored (arrowed) shell viewed ventrally, dorsally and anteriorly. Avontuur. BD6712. 21–23, × 1·5. 24, detail of the anterior margin showing tubercules through the gape. × 4.


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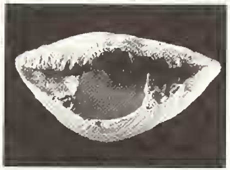
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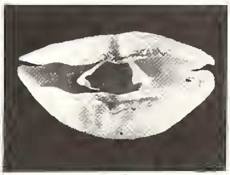
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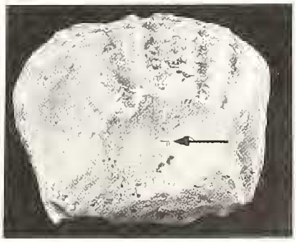
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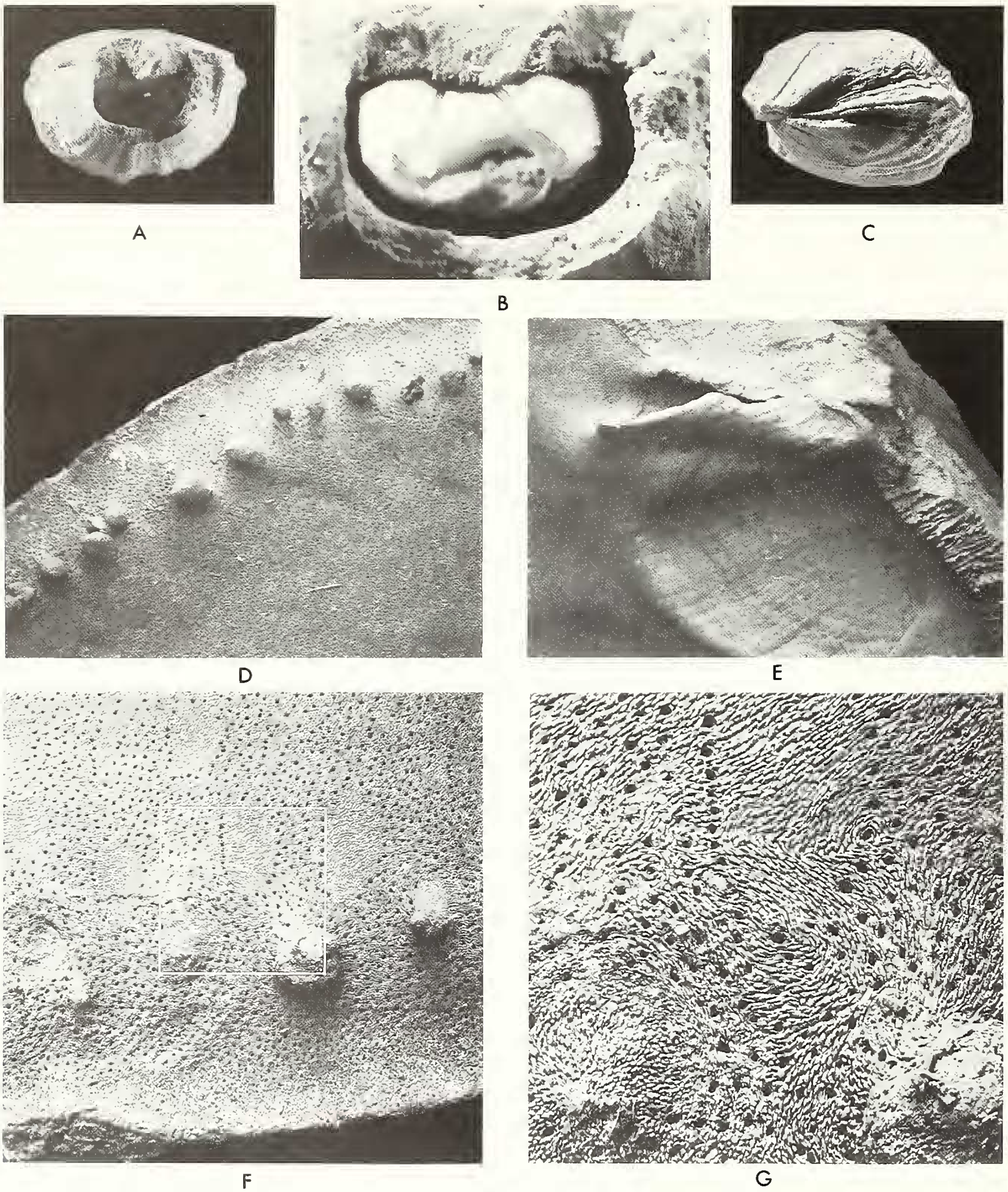
BRUNTON and HILLER, Namaqualand brachiopods



TEXT-FIG. 6. *Kraussina rotundata* sp. nov. from Avontuur – T3. A, C, a large shell viewed posteriorly (A) and laterally (C) showing posterior abrasion and lateral growth distortion, BD6713, × 1.5. B, enlarged posterior view of the pedicle aperture using bottom lighting to show the lophophore support within the shell, × 5. D–G, scanning electron micrographs (not coated, environmental chamber) of the interior of a brachial valve, BD6714. D, tubercules at the posterolateral margin, × 19. E, part of the cardinalia showing a socket, part of the radially ridged cardinal process and part of the pedicle adjustor muscle scar, × 12. F, tubercules at the anterior margin displaying resorption and regeneration patterns, × 42. G, detail from the centre of F showing the shell mosaic in an area of recent resorption and two current tubercules, × 130.

Kraussina rotundata sp. nov.

Plate 3, figs. 1–24; Text-figs. 6–8

Diagnosis. Strongly biconvex *Kraussina* ornamented by relatively few, medianly developed, coarse costae.

Type. Holotype BD6705. Paratypes SAM PQ AV 609, AV 610; SAM PQ HB 217, HB 348, and eight figured shells, BD6706–BD6714 (excluding BD6711), from Avontuur A.

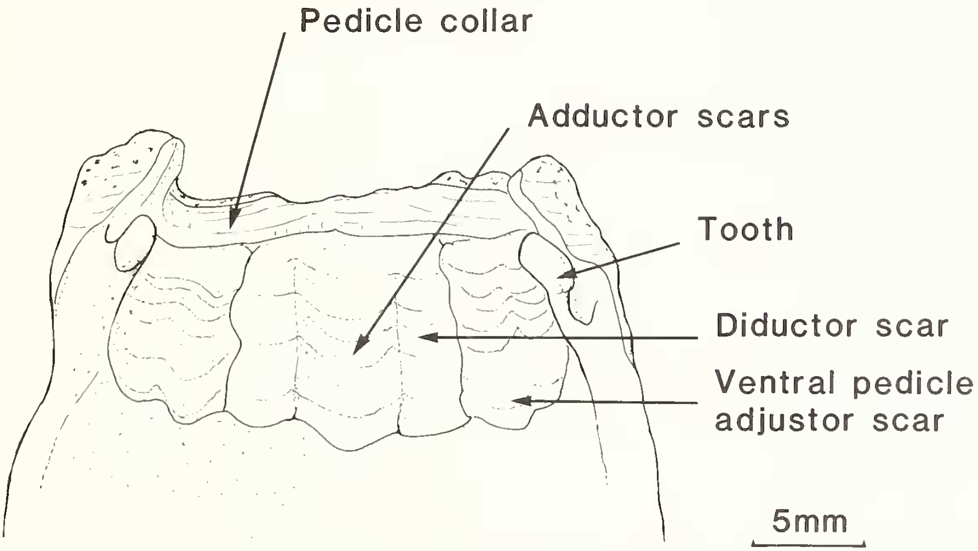
Name. Rotundus (L.) = round, spherical, referring to the strong biconvexity of the shell.

Material and horizon. Thirty-three conjoined valves, nine pedicle valves and eight brachial valves all from the 50 m Unit on Hondeklip and Avontuur A. Three shells and a few incomplete valves in the Carrington collection.

Description. Strongly biconvex shells with subcircular outlines; the length usually slightly greater than width, although shape can be variable. The hinge line is nearly straight, about four-fifths as wide as the valve. The anterior commissure is rectimarginate to broadly and gently sulcate. The beak is suberect with a very large submesothyridid foramen; posterior margins of shells are often abraded away by movement against hard substrates. The ornament consists of concentric growth lines and a few coarse subangular costae developed medianly. Ribs extend from the umbo but are often abraded from posterior portions of the valves; ribbing density of one to four ribs in one, twelve, four and one specimens at 5 mm medianly at the 10 mm growth stage, although a few shells show minimal ribbing; lateral areas are devoid of ribbing. Shell substance is thick, compared to *K. rubra*.

The pedicle valve is strongly convex in anterior and lateral profiles. Brachial valves are convex in lateral profile, and also in anterior profile but with a slight median flattening or incipient sulcus development.

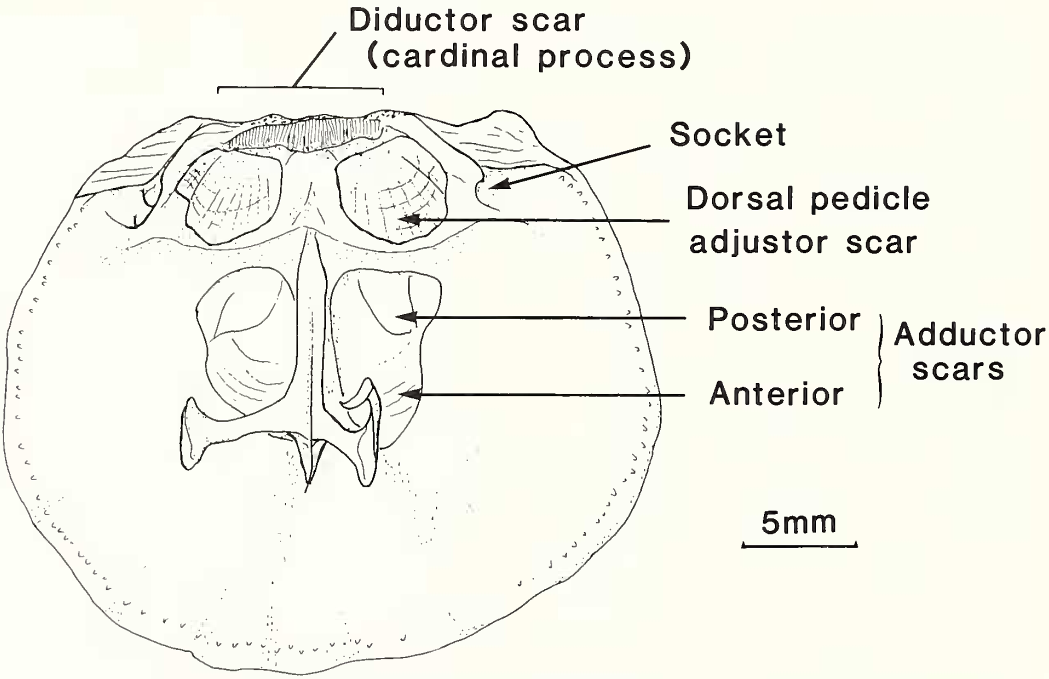
The pedicle valve interior has small, robust and strongly cyrtomatodont teeth. The pedicle collar is short, commonly sessile, but rarely free anteriorly resulting from anterior growth as a consequence of posterior abrasion. The ventral pedicle adjustor muscle scars are prominent, somewhat quadrate areas positioned posterolaterally, below the thickened shell of the teeth supports; they are commonly ridged concentrically (text-fig. 7). Between these scars is a slightly concave ovate area, somewhat thickened anteriorly and laterally, which extends forwards to a position just in front of the anterior edges of the adjustor scars; this is the scar



TEXT-FIG. 7. Drawing of the posterior internal region of a pedicle valve of *Kraussina rotundata* sp. nov. showing the dispositions of the muscle attachment areas.

of the relatively small adductor muscles which, unlike their dorsal ends, are a closely united pair. The diductor muscle scars are weakly impressed, but positioned between the adductor and adjustor scars. (This interpretation is based upon study of the muscles in Recent *K. rubra*, with very similar muscle scars to *K. rotundata*.) Within about 0·5 mm of the valve margins are small outwardly directed tubercules with a frequency of about sixteen per 5 mm of valve edge. Their preservation is variable, due largely to the periodic resorption and overgrowth of the tubercules during valve growth and thickening (text-fig. 6D, F, G).

The brachial valve interior has short, thick widely divergent socket ridges bounding small narrow sockets. The cardinal process is transversely elliptical, situated between the posterior ends of the socket ridges but often is partially removed by abrasion of the posterior shell margin. A broadly triangular notothyrial platform serves for the attachment of pedicle adjustor muscles, marked by a pair of ovoid to quadrate scars; from the anterior margin the low median septum extends to little more than one-half of the valve length (text-fig. 8). The distal end of the septum supports a pair of ventrally diverging brachial lamellae; the ventral end of each lamella widens as it bends posteriorly then narrows to a prong curving ventromedianly (Pl. 3, figs. 3 and 11). Elliptical to oblong adductor scars are impressed on the valve floor on either side of the median septum, between the notothyrial platform and the brachidium; small subcircular posterolateral elements of the scars are differentiated and show where the smaller posterior adductor muscles were attached. Submarginal tubercules are more strongly and commonly present than in pedicle valves.



TEXT-FIG. 8. Drawing of a brachial valve interior of *Kraussina rotundata* sp. nov. showing the morphology and main muscle attachment areas.

Dimensions. Examples of the dimensions of conjoined valves are (in mm):

	Length	*Width*	*Hinge w.*	*Thickness*	
Holotype	22·5	22·4	19·1	15·2	BD6705
Paratypes	16·3	17·5	13·6	9·2	BD6706
	19·4	20·7	17·1	10·8	BD6712
	22·5	21·9	16·1	15·4	BD6713
	23·0	19·6	*c.*12·0	12·5	BD6709
	24·0	23·0	17·0	17·0	BD6707

Discussion. The shells described here are immediately referable to *Kraussina* on the basis of their internal structures, but they differ from other species of the genus in several important respects. Their coarseness and distribution of ribbing immediately separates them from the living species *K. rubra*, *K. cognata*, *K. gardineri* and *K. crassicostata*. *K. mercatori* from off the west African coast, is a form that does not develop any ribs and, although many of the present specimens are sparsely ribbed, the normal form of the shell is with ribs developed medianly and thus they can be separated from *K. mercatori*, which is also smaller and with a coarsely tubercular valve interior.

Of the fossil species, only *K. lata* has a similar density of ribbing to *K. rotundata* sp. nov. but it has ribs strongly developed over the entire valve surface. In addition, *K. lata* has a flatter brachial valve and is usually wider than long with maximum width at or near the hinge line and rather acute cardinal angles (Haughton 1932).

Kraussina laevicostata sp. nov.

Text-fig. 9A–H

Diagnosis. Large, transverse, ventribiconvex *Kraussina* lacking persistent ribbing.

Types. Holotype: BD6730, an incomplete shell (text-fig. 9A–C). Paratypes: two pedicle valves and an incomplete brachial valve from Koingnaas. Five incomplete brachial valves and one pedicle valve from the 'E Stage', Carrington collection.

Name. Laevis (L.) = smooth or bald. Costa (L, f) = rib, referring to the scant ribbing.

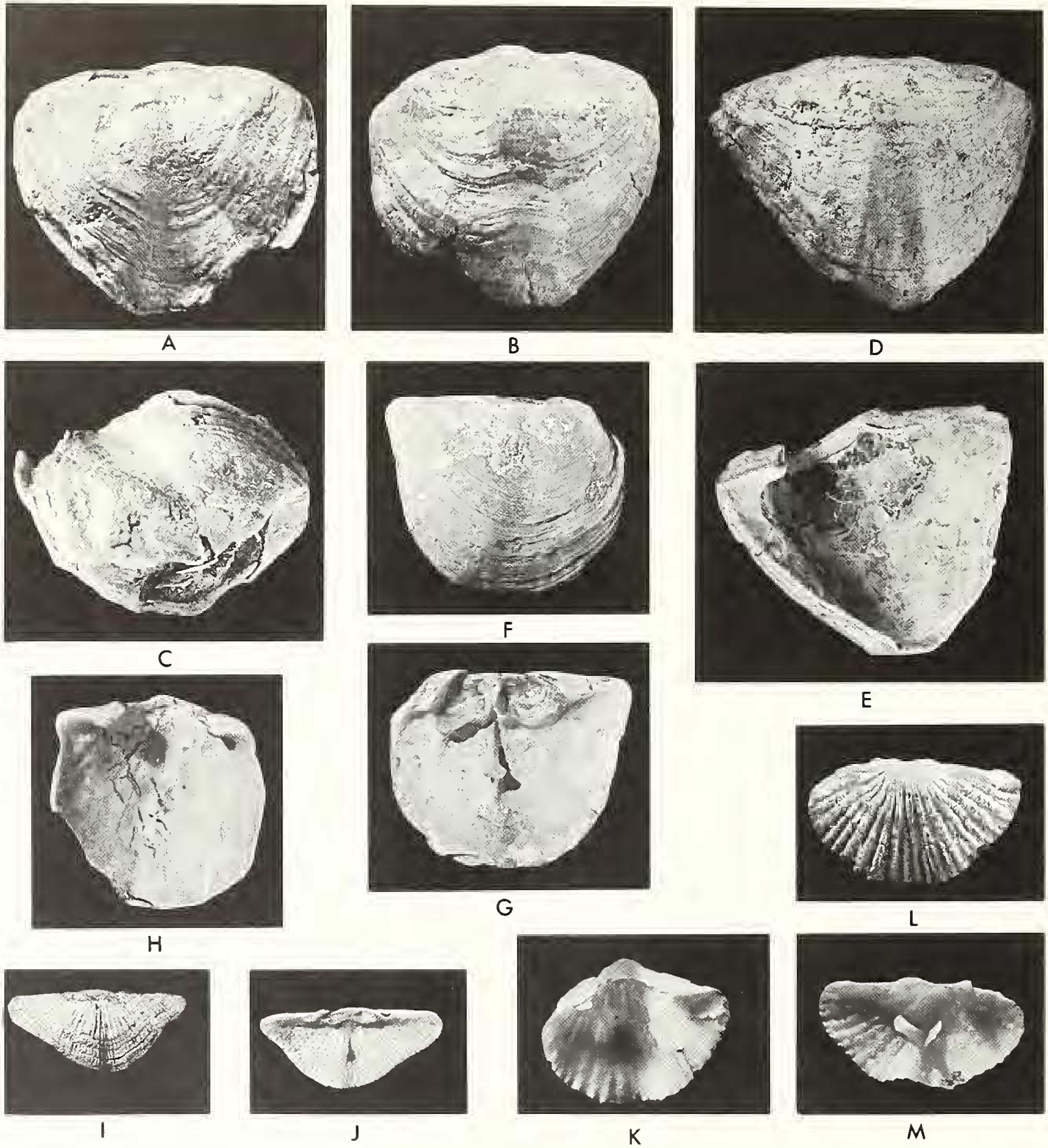
Description. The outline is very broadly obovate, with a hinge line almost reaching the maximum width. The lateral profile is ventribiconvex, the brachial valve being almost flat to gently convex, with a sulcus starting about 10 mm from the umbo. There is a complimentary fold on the pedicle valve producing a gently sulcate anterior commissure. The pedicle aperture is wide, abraded ventrally, and bordered by variably developed interareas. External ornamentation is of prominent growth lines, especially anteriorly, and irregular, impersistent occasional median ribs, developed only after about 30 mm in length.

Pedicle valve interiors have relatively small teeth, which in older specimens are supported by shell thickening below the interareas. There is a short pedicle collar which, in some specimens, is partially worn away. Muscle scars are typically kraussinid. In large shells they are slightly sunken into the valve floor; the laterally placed adjustor scars are more prominent. Brachial valve interiors are similar to those of *K. rotundata*, but in adults the prominent adjustor scars are less widely separated and elevated medianly. Both valves have submarginal tubercules with a frequency of ten to sixteen per 5 mm.

Dimensions (in mm)	*Length*	*Width*	*Hinge w.*	*Thickness*	
Holotype, shell	37·4	42·5	40·8	21·1	BD6730
Paratypes b.v.	28·0	33·6	32·6	—	BD6732
p.v.	30·5	30·4	26·6	—	BD6733
p.v.	35·8	47·4	44·8	—	BD6731
p.v.	40·6	38·9	*c.*37·6	—	BD6734

Discussion. This large species is comparable in size to the largest, wide example of *K. lata*, but the two differ in that the latter is strongly ribbed. *K. laevicostata* would seem to have had the same high degree of shape variation as is seen in the more numerous *K. rotundata*. The sulcate commissure developed early in life and the ventral fold may be accentuated by what resembles a pair of ribs (text-fig. 9D). However, these do not seem to be present on brachial valves.

In present-day waters off South Africa there is a ventribiconvex species, virtually lacking ribs, *K. cognata* (Sowerby), which is smaller and much less transverse than *K. laevicostata*. It is possible that size and relative width reduction may have transformed *K. laevicostata* into *K. cognata*.



TEXT-FIG. 9. A–H, *Kraussina laevicostata* sp. nov., A–C, Holotype viewed dorsally, ventrally and posterodorsally, Koingnaas, BD6730. D, E, a pedicle valve viewed externally and obliquely internally showing the pedicle collar and pedicle adjustor muscle scar flanking the diductor and median adductor scars, Koingnass, BD6731. F, G, a smaller brachial valve exterior and interior with a distorted right ear. Carrington collection, E stage, BD6732. H, an incomplete pedicle valve interior. Carrington collection, E stage, BD6733. All × 1. I–M, *Kraussina cuneata* sp. nov., from Koingnaas. I, J, a brachial valve exterior and interior, BD6738, × 1·5. K–M, holotype, a complete shell with separated valves, BD3739, × 4·5. K, pedicle valve interior showing the teeth and pedicle collar. L, M, brachial valve exterior and interior, showing the tuberculate interior and small inner socket ridges.

Kraussina cuneata sp. nov.

Text-fig. 9I–M

Diagnosis. Small, transverse, entirely finely ribbed *Kraussina* with persistent dorsal sulcus.

Types. Holotype BD6739 (text-fig. 9K–M) and ten other incomplete valves from the Carrington collection, E stage.

Name. Cuneatus (L.) = wedge-shape, or inverted triangle, referring to the shell's outline.

Description. These small shells (5–10 mm long) are broadly rounded triangular in outline, some reaching twice as wide as long. The greatest width is just anterior to the hinge line. The lateral profile is ventribiconvex. The dorsal sulcus is shallow, but originates close to the umbo. The ventral fold is less clear, but the anterior commissure is sulcate. The pedicle aperture is large and the interareas short but broad, small triangular deltidial plates may be preserved.

The external ornamentation is of periodical growth-halts plus fine, regular ribbing over the complete shell. Brachial valve costellae are added by intercalation. There are twelve to sixteen ribs per 5 mm width at 10 mm in three, one, two, five and one specimens. The pedicle valve interior has small cyrtomatodont teeth and a relatively long sessile pedicle collar. Muscle scars are ill-defined on the few available specimens, but appear to be as in *K. rotundata.*

Brachial valve interiors have small widely divergent sockets, almost confined to the thickened posterior margin of the valve. The cardinal process is very short, but wide and typically radially ridged. The notothyrial platform is short and wide, accommodating transversely elliptical pedicle adjustor muscle scars. The median septum is low posteriorly, reaching about one-half of the valve length, and branches ventrolaterally into the main V-shaped brachidium; the complete structure is unknown. Adductor muscle scars are positioned normally, but poorly differentiated.

The interiors of both valves display, to a variable extent, the form of the external ribbing and radial lines of tubercles following the rib interspaces. Close to the valve margins are more prominent tubercules with a frequency of between 9 and 13 per 5 mm length of margin.

Dimensions (in mm)	*Length*	*Width*	*Hinge w.*	
Holotype, shell	5·1	6·8	6·0	BD6739
b.v.	8·0	16·5	15·1	BD6738
b.v.	8·0	14·2	12·6	BD6740
p.v.	9·9	14·6	13·7	BD6741
p.v.	7·5	11·8	10·8	BD6771

Discussion. These small shells in some respects resemble *Megerlina*, but cannot be assigned to that genus because they show no sign of the pair of wing-like lateral extensions from the V-shaped part of the brachidium characteristic of *Megerlina.* The transverse outline, although much smaller, is comparable to the wide variety of *K. lata* from the Carrington collection. However, although some *Kraussina* specimens display an initial 4 mm of ribbing finer than that covering the adult valves, the ribbing covering the valves of *K. cuneata* is still finer than any seem on other *Kraussina* species in these faunas. The persistent dorsal sulcus and internally developed tubercules also differentiate this species.

Superfamily CANCELLOTHYRIDACEA Thomson, 1927
Family CANCELLOTHYRIDIDAE Thomson, 1927
Subfamily CANCELLOTHYRIDINAE Thomson, 1927
Genus CANCELLOTHYRIS Thomson, 1927

Cancellothyris platys sp. nov.

Plate 4, figs. 1–13; Text-fig. 10A–G

Diagnosis. Large, relatively broad, rectimarginate to uniplicate *Cancellothyris* with thickness just over one-half length of shell.

Types. Holotype, BD6742, from the 50 m Unit at Avontuur A. Paratypes, figured specimens from Avontuur A and Hondeklip.

Name. Platys (Gr.) = broad, wide.

Material. In addition to the type specimens, there are fourteen shells from Avontuur A, plus two pedicle valves and two brachial valves; from Hondeklip there are two pedicle and three brachial valves; and in the Carrington collection there are two small shells, three pedicle and three brachial valves, mostly marked 'B-1', all of which are somewhat eroded.

At the Koingnaas locality were recovered two shells, two pedicle and three brachial valves, all in an incomplete state of preservation, representing the large and wide sub-species, *C. p. petalos* nov. (See the discussion.)

Description. The outline is approximately five-sixths as wide as long, the greatest width being at about two-thirds the total length and the anterior margin being widely rounded. The lateral profile is biconvex, with a prominent ventral umbo truncated by the large pedicle foramen, commonly slightly widened by abrasion. Deltidial plates are medianly joined and short. The lateral commissure rises slightly anteriorly, and the anterior margin is rectimarginate to gently uniplicate in specimens over about 30 mm long. Thus in brachial valves over about 28 mm long a slight marginal fold developed.

External ornamentation is of growth lines and a well developed fine ribbing, with 12–17 ribs in a width of 5 mm at 20 mm from the dorsal umbo in one, ten, six, six, two and one specimens. Even the larger uniplicate specimens show only the slightest folding or sulcation on their valves.

Internally the pedicle valve has strong cyrtomatodont teeth supported by shell thickening on the flanks of the umbonal cavity. There is a well developed pedicle collar, free anteriorly and capable of growth into a short tube (text-fig. 10F). Muscle scars are ill defined, but the diductors are large and spreading.

In the brachial valve umbo there is a narrow, ridged cardinal process from which sockets widen anterolaterally, with strong inner socket ridges overhanging the sockets posteriorly. The floor of the functional anterior part of the socket is supported by thickening from the inner surface of the valve (Pl. 4, fig. 9). From the anteromedian corners of the sockets crura extend anteromedianly, as if to meet at about two-thirds of the brachial valve length. They are, however, only a few mm long before branching to form the complete ring of the brachidium (Pl. 4, figs. 4 and 5). The anterior transverse band is relatively wide, ventrally arched and convex anteriorly. Muscle scars are not clearly differentiated. The median diductor scars are oblong, with rounded anterior margins, and flanked by widely spreading pedicle adjustor scars.

Dimensions (*in mm*). (All but one being from complete shells)

	Length	*Width*	*Thickness*	
Holotype	33·5	29·7	18·9	BD6742
Paratypes	36·2	29·9	20·6	BD6745
	34·3	29·1	18·6	BD6743
	37·9	28·3	19·4	BD6744

EXPLANATION OF PLATE 4

Figs. 1–14. *Cancellothyris platys platys* sp. et subsp. nov. 1–5, holotype, the complete shell viewed ventrally and dorsally. The separate pedicle valve internally and the brachial valve internally and oblique internally. Avontuur. BD6742. × 1. 6–10, a complete shell from Hondeklip. BD6743. 6–8, viewed ventrally, dorsally and laterally. × 1. 9, the cardinalia and pedicle valve umbo (above). × 3. 10, the umbos of the shell externally showing the deltidial plates and slightly abraded pedicle aperture. × 6. 11, lateral view of a shell with growth distortion (arrowed) at its lateral commissure. Avontuur. BD6744. × 1. 12–14, a complete shell with, internally, its loop and some of the associated spiculation preserved and protruding from the sand which filled the shell. Avontuur. BD6745. 12 and 14, the open shell viewed anterolaterally and closed, from the other side. × 1. 13, a detail from fig. 12 showing the anterior portion of the brachial loop (arrowed) and, anterior to that, a large remnant of the spicular skeleton that helped support the lophophore beyond the loop. × 10.

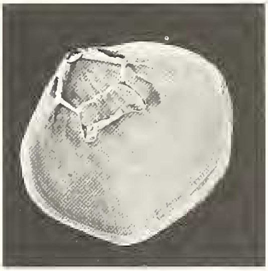
PLATE 4


1


2


3


4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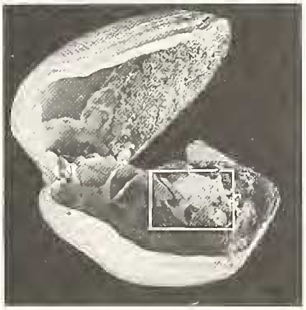
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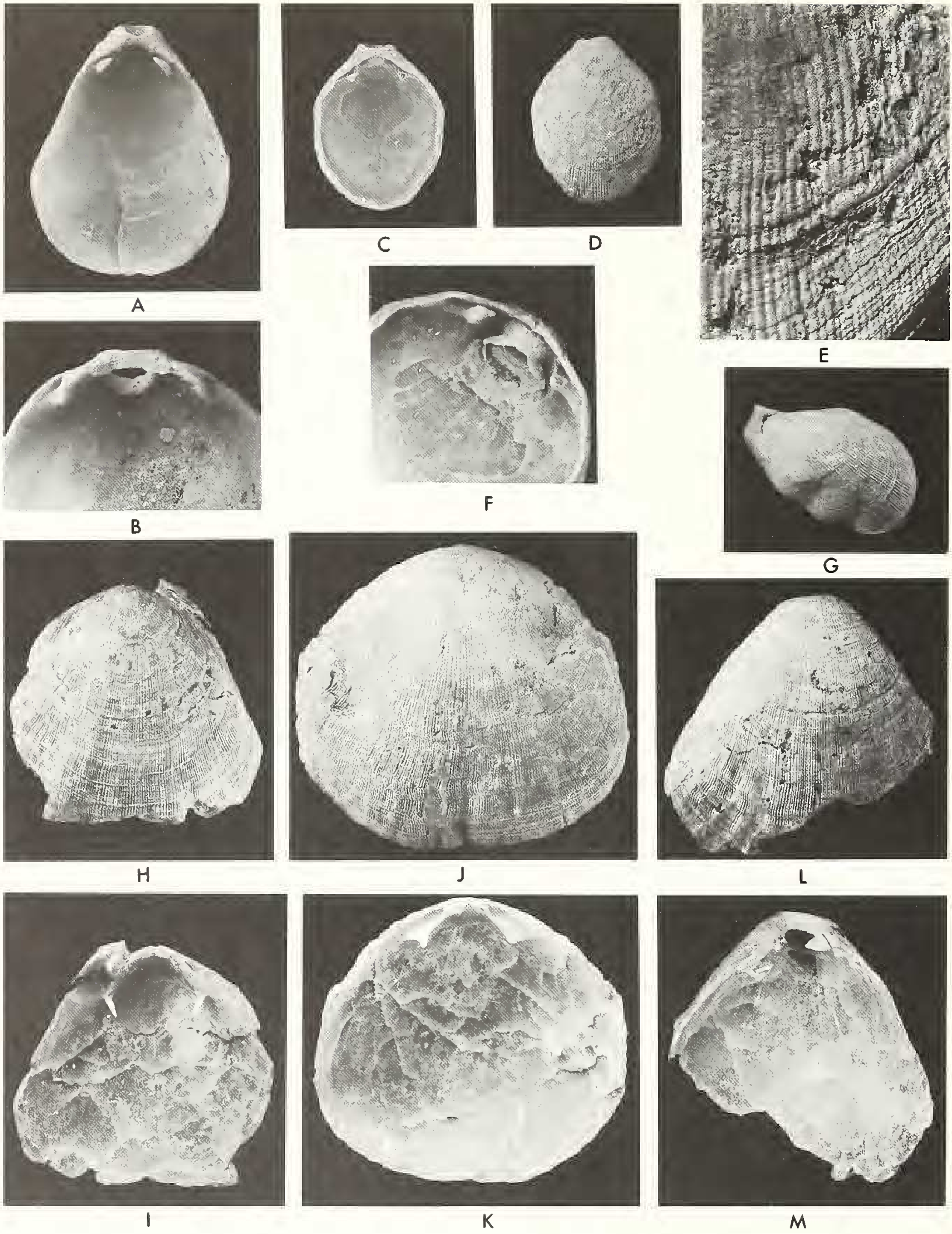
14

BRUNTON and HILLER, Namaqualand brachiopods



TEXT-FIG. 10. For legend see opposite.

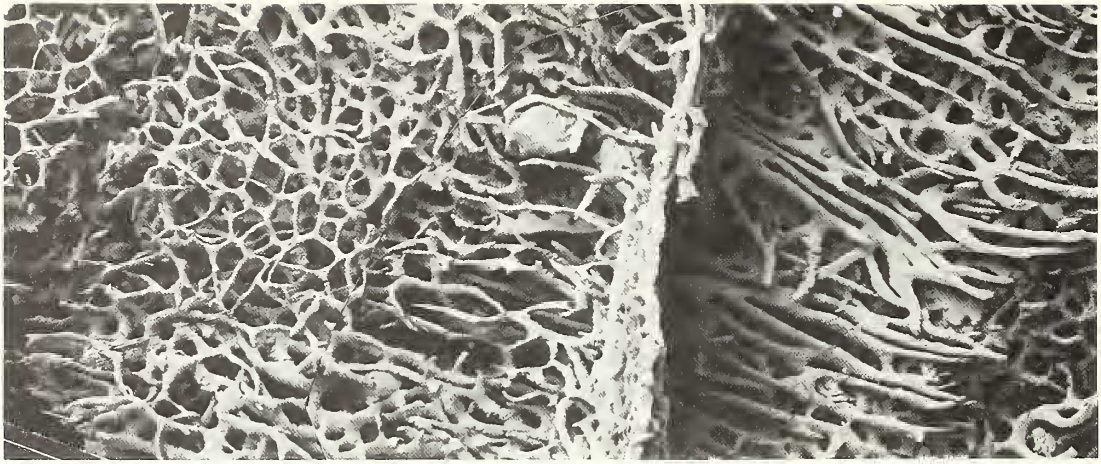
p.v.	37·9	30·4	—	BD6746
	36·8	31·6	21·5	BD6751
	30·5	30·4	16·7	BD6752
	32·4	27·5	15·3	BD6753
	28·8	26·3	13·0	BD6754
	15·8	13·9	10·7	BD6755
	16·0	14·8	8·3	BD6756

Discussion. Living *Cancellothyris* appears to be restricted to Australian waters and taxonomically the nearest species now living in South African waters are *Terebratulina abyssicola* (Adams and Reeve), *T. meridionalis* Jackson 1952 and *Terebratulina* species of Cooper (1973*b*), Hiller (1986) and Jackson (1952). The main distinction between *Cancellothyris* and *Terebratulina* is the conjunct deltidial plates in the former, but Cooper (1973*a*) has commented that *T. abyssa* [error for *abyssicola*] from off South Africa may occasionally have united deltidial plates. Cooper's observation raises a question of validity of these two genera, and also provides a clue that this cancellothyrid morphology of conjunct plates may be retained in the South African populations. *C. platys* differs from *T. abyssicola*, as originally described, by being very much larger. However, as pointed out by Jackson (1952), the original Adams and Reeve (1850) specimen is probably young and those figured by Jackson reached 28·4 mm long. Apart from the non-conjunct deltidial plates, Jackson's *T. abyssicola* specimens have a prominent dorsal sulcus, producing a sulciplicate anterior commissure. The loops of Jackson's examples and those of *C. platys* are very similar.

C. platys is most abundant at the Avontuur A locality. Shape variation is not extreme, but a few specimens did grow in confined conditions, leading to growth distortions (text-fig. 10G). Most of these distortions affected relatively short lengths of the valve margins and in one shell (Pl. 4, fig. 11) possibly led to its shift in position away from the confining object and consequential extra abrasion at the left side of the pedicle aperture. We believe it more likely that these distortions resulted from growth against hard substrate rather than against other specimens. An unusual feature in some pedicle valves is the extent of anterior growth of the pedicle collar (text-fig. 10C, F). This does not seem to be associated with particularly severe abrasion of the pedicle aperture, as might be expected.

Within the coarse sands and fine shelly debris filling specimens of *C. platys* we have recovered some small fragments of the original spicular skeleton which supported the lophophore. The complexity and stability of these structures are to be expected in this species, in view of the spicules studied in living *Terebratulina* by such authors as Deslongchamps (1860), Blochmann (1912) and Schumann (1973). Spicules have been described previously from fossil brachiopods, for example by Steinich (1963) from the Cretaceous and by Rowell and Rundle (1967) in Eocene *Terebratulina*, but seldom with as good preservation or articulation as here. In one specimen the entire mesodermal spicular skeleton has slipped anterolaterally from its original position on the loop and lies, somewhat crushed, within the sediment; those parts from the loop area and one side arm of the lophophore can be seen (Pl. 4, figs. 12 and 13). The features which strikingly differentiate these spicules from those previously figured from *Terebratulina* are their length and intricate intermeshing, each part of the skeleton being made up of many layers of interlocked spicules (text-fig. 11).

TEXT-FIG. 10. A–G, *Cancellothyris platys platys* sp. et subsp. nov. from Avontuur, A, B, a pedicle valve interior showing conjoined deltidial plates and teeth (× 1) and a detail of the umbo internally showing the pedicle collar (× 2·5) BD6746. C–F, a pedicle valve, BD6747. C, viewed internally showing the well differentiated muscle field, × 1. D, external view, × 1, E, part of the external view enlarged to show the effect of surface borings, × 5. F, the internal posterior region showing the unusually lengthened pedicle collar, the teeth, and the wide adductor and diductor muscle scars, × 2. H–M, *Cancellothyris platys petalos* sp. et subsp. nov. from Koingnaas, × 1. H, I, an incomplete brachial valve exterior and interior with the tooth from the pedicle valve remaining in position on one side, BD6749a. J, K, holotype of the subspecies, a brachial valve viewed externally and internally, BD6750. L, M, the pedicle valve, viewed externally and internally, belonging to the brachial valve figured H, I. Deltidial plates have mostly been broken away when the shell was slightly crushed within the sediment, BD6749b.



TEXT-FIG. 11. Scanning electron micrographs of part of the spicular lophophore support recovered from an example of *Cancellothyris platys* sp. nov. from Avontuur. This area is thought to have been associated with the anterior transverse band of the loop, the long elements on the right being associated with the lophophore canals and the reticulated area on the left being part of the central support between the lophophore arms. BD6767. ×75.

At the Koingnaas locality there are several incomplete specimens which are larger (around 50 mm long) and relatively wider (the length and width being approximately equal) than the normal *C. platys*. Growth lines indicate that this shape was more or less consistent throughout life and that this extra width is not simply a gerontic feature. The rib density is comparable to the other specimens. Since these specimens became broader than true *C. platys* at an early stage of life it is not surprising to find the relative width of the crural bases (text-fig. 10I) is greater than in *C. platys*. We treat these specimens as a subspecies, *C. platys petalos* (text-fig. 10H–M)

Dimensions (in mm)		*Length*	*Width*	*Thickness*	
Holotype	b.v.	48·0	53·0	—	BD6750
Paratypes	p.v.	*c*.53·9	*c*.51·5	—	BD6764
	shell	51·5	46·4	*c*.23·8	BD6765
	shell	50·3	*c*.46·3	28·6	BD6766

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